Aquatic Botany, 11 (1981) 1—9
Elsevier Scientific Publishing Company, Amsterdam — Printed in The Netherlands

SEASONAL PATTERNS OF PLANT AND SOIL WATER POTENTIAL ON AN IRREGULARLY-FLOODED TIDAL MARSH

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(Accepted 18 November 1980)

ABSTRACT

De Jong, T.M. and Drake, B.G., 1981. Seasonal patterns of plant and soil water potential on an irregularly-flooded tidal marsh. *Aquat. Bot.*, 11: 1—9.

Water potential (ψ_p) of five plant species and soil water potential (ψ_s) in their respective communities were measured before dawn once a week throughout the 1978 growing season on an irregularly flooded tidal marsh on the Rhode River of the Chesapeake Bay. The five species exhibited two different seasonal patterns of ψ_p. Two species (*Scirpus olneyi* Gray and *Scirpus robustus* Pursh) had pre-dawn $\psi_p \geqslant -5$ bar throughout the entire growing season; and three species (*Iva frutescens* L., *Spartina cynosuroides* (L.) Roth and *Panicum virgatum* L.) had ψ_p that ranged between -5 and -15 bar. Although there were consistent differences between the ψ_s of the plant communities at 50 cm and within 10 cm of the marsh surface, these differences were small (< 4 bar) and the mean ψ_s of all communities on the marsh was always higher than -8 bar. The correspondence between plant distribution, ψ_p, and ψ_s was not as expected: species with the lowest ψ_p were found in the communities having the highest ψ_s.

INTRODUCTION

The influence of salinity on the distribution of coastal tidal marsh species has been studied by many investigators (Penfound and Hathaway, 1938; Chapman, 1940, 1960; Purer, 1942; Adams, 1963; Mendelssohn and Marcellus, 1976; Hackney and De La Cruz, 1978). Although clearcut correlations between species distribution and salinity have often been difficult to demonstrate (Adams, 1963; Hackney and De La Cruz, 1978), it has been shown that certain species have greater tolerance to salinity than others (Penfound and Hathaway, 1938; Barbour and Davis, 1970; Parrando et al., 1978), and it is generally believed that salinity plays a role in the distribution of tidal marsh species (Harshberger, 1911; Chapman, 1960;

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Mall, 1969; Cooper, 1974; Mendelssohn and Marcellus, 1976). Previous ecological studies regarding the water or salinity relations of tidal marshes have primarily relied upon measurement of marsh water salinities and correlations between species distributions or growth tolerances and the ranges of salinities measured (Harshberger, 1911; Penfound and Hathaway, 1938; Chapman, 1940, 1960; Purer, 1942; Adams, 1963; Hackney and De La Cruz, 1978). Although such research may indicate the importance of salinity in species distributions, it does not provide data on the availability of water to the plant or the development of water stress within different plant species.

Seasonal increases in soil salinity can be expected to exert two different types of effects on the physiology of marsh plants, i.e. those associated with ion toxicity and those related to soil water (and by inference, plant water) potential. The authors have restricted this study to determining the seasonal patterns of soil and plant water potential. Measurements were taken at dawn, in order to avoid daytime drying which was expected to vary greatly from day to day. The focus of primary interest was the seasonal patterns which might be obscured by the range of plant water potentials associated with a broad range of daily atmospheric humidity. Although it might be supposed that sufficient water is available in a salt marsh to meet the demand of evapotranspiration, there is evidence of the seasonal development of hypersalinity in some marshes (Chapman, 1960), which implies low soil water potential. Since sea water has a water potential less than −20 bar, plants exposed daily to this or more negative water potential, must develop even lower water potential and this means that water stress may be an important factor in species distribution in salt marshes. Plant water potential (ψ_p) and soil water potential (ψ_s) were measured in four salt-marsh communities to determine whether there are differences between ψ_p of different salt-marsh species that correspond to the differences between the ψ_s of the communities in which the plants are found.

MATERIALS AND METHODS

Research was conducted in the Kirkpatrick Marsh, located at the Chesapeake Bay Center for Environmental Studies (CBCES) on the western shore of the Chesapeake Bay (38° 53′ N, 76° 33′ W). Kirkpatrick Marsh forms the southern margin of Muddy Creek which flows into the Rhode River estuary. The section of marsh in which the study was conducted is similar to what is sometimes referred to as a 'high marsh' (Cooper, 1974), or 'irregularly flooded marsh' (Waits, 1967) and which is called the 'mixed community' here. The biomass of the sedge, *Scirpus olneyi* Gray, is about 50% of the total biomass of the community. The remaining 50% is composed of the two grass species, *Spartina patens* (Ait.) Muhl. and *Distichlis spicata* (L.) Greene. During the year in which this study took place *Pluchea purpurascens* (Swartz) DC., *Cyperus odoratus* L., *Solidago sempervirens* L. and *Kostelet-*

skya virginica (L.) Presl were occasionally present in the mixed community. In the remainder of this paper, the communities that border the mixed community are referred to as the 'creek bank' and 'forest margin' communities so as to distinguish them from the 'central' marsh community. The margin of the marsh adjacent to the forest is a narrow strip of vegetation dominated by *Panicum virgatum* L. and *Scirpus robustus* Pursh with an occasional *Hibiscus palustris* L. and a number of other species commonly found on the edge of high marshes. Along another margin, adjacent to a small creek, there is a community dominated by *Iva frutescens* L. where *Spartina cynosuroides* (L.) Roth, *Kosteletskya virginica*, *Amaranthus cannabinus* (L.) Sauer, *Scirpus olneyi*, and *Solidago sempervirens* are also common.

The root mat is ca. 30 cm deep in the communities studied. In order to examine the water potential of soil water near the roots, samples were taken at a depth of 10 cm from the surface. The soil water was also sampled below the roots (at 50 cm depth) to determine whether or not a gradient in water potential is established between water at this depth and the root mat. Soil water at these two depths was sampled weekly between May 10 to September 27 1978. Sampling stations were set up in each of the three community types across the marsh. At each station a core 3.2 cm in diameter and 50 cm in depth was removed from the marsh soil and replaced with a 3.2-cm diameter p.v.c. pipe which extended 50 cm into the marsh soil and 100 cm above the soil, and served as a small well. Samples of soil water were taken from 50 cm depth in the following manner. Each well was pumped dry and allowed to refill. A 10-ml sample was then collected from the bottom of the well and stored in a 20-ml glass vial until measurements of ψ_s were made. For the measurement of ψ_s at 10 cm depth, cores of marsh sod were collected near the wells at each of the 12 stations, and subsamples of these cores were stored in 20-ml vials.

The ψ_p of five plant species was measured weekly. Samples of tissue were taken just at dawn for two reasons: first, it was desired to avoid variations in ψ_p from day-to-day resultant from variations in the demand upon transpiration; and second, it was desired to compare ψ_p of different species at a time when recovery from day-time water stress would have occurred to the fullest extent. Two samples of *Scirpus olneyi* were collected at each of two locations in the mixed community. Three samples each of *Panicum virgatum*, *Scirpus robustus*, *Iva frutescens* and *Spartina cynosuroides* were collected near the stations within the marginal communities.

Leaves to be sampled were first rinsed with distilled water to remove surface salt and debris. Water remaining on the leaf surface after rinsing was blotted dry with tissue paper. No effort was made to select leaves of a specific age, but fully developed leaves were chosen. Since the sedge *Scirpus olneyi* has no leaves, it was necessary to use the culms.

The ψ_p and ψ_s were measured with 12 leaf-cutter thermocouple psychrometers (J.R.D. Merrill Specialty Co., Logan, UT, U.S.A.) in a field laboratory at the study site. The psychrometers were taken onto the marsh and attached tissue was placed between the leaf-cutter psychrometer and a clean rubber stopper. A small section of the tissue was then cut and immediately sealed into the psychrometer chamber. ψ_s was measured for the 50 cm depth by saturating a 0.5-cm diameter filter paper disc with the soil water and placing it into the psychrometer chamber. ψ_s from the 10 cm depth was measured by placing approximately 0.5 g of the marsh soil directly into the psychrometer chamber. The loaded psychrometers were totally immersed into the inner bath of a double water bath. The outer bath of the double water bath was stirred and maintained within ±0.1°C of the set temperature, 35°C, with an immersion heater and a temperature controller (Yellow Springs Inst., Model 63RC). The inner bath was totally surrounded by the water of the water bath, but no water was allowed to be exchanged between the two baths while the psychrometers were in the inner bath. The psychrometers were allowed to equilibrate in the water bath for 3—12 h. The maximum equilibration time required for readings to become stable was determined to be ca. 2.5 h, which is in agreement with Brown (1972). Measurements were therefore made after a 3 h equilibration period. The thermocouple psychrometers were read with the use of a switch box (J.R.D. Merrill Specialty Co., Model No. 82-20), a custom built amplifier, and a strip chart recorder (Hewlett Packard Model 7100B). Each thermocouple psychrometer was individually calibrated with a series of five KCl solutions (Brown, 1972).

RESULTS

Precipitation

Table I shows the monthly precipitation totals for 1978 and their deviation from the norm calculated over a 20-y period at the Annapolis Police Barracks in Annapolis, Maryland, which is the nearest U.S. Department of Commerce Climatological Station to the study site, and although it is ca. 15 km from CBCES, the data from there are similar to unpublished rainfall records collected at CBCES. These data indicate that January, March, May, July, August and December were months of relatively high precipitation, whereas during February, April, September and October, precipitation was below the 20-y norm. The total yearly rainfall was approximately 10% greater than the 20-y norm. There is little to suggest that rainfall during 1978 was anything other than normal.

Soil water potential

The mean ψ_s at 50 cm did not vary by more than 3 bar for any given community type during the entire sampling period (Fig. 1). There were small but consistent differences in the mean ψ_s between the four community types.

TABLE I

Monthly precipitation data during 1978 and departure from the norm (calculated over the previous 20 y*)

Month	Monthly total (cm)	Departure from norm (cm)
January	21.2	14.1
February	1.2	−5.5
March	11.6	2.5
April	4.0	−4.0
May	16.2	7.3
June	6.4	−2.4
July	12.5	2.7
August	11.3	1.0
September	4.7	−3.1
October	2.3	−4.0
November	5.4	−2.3
December	13.7	5.3
Total for 1978	110.8	11.6

*Data from U.S. Department of Commerce.

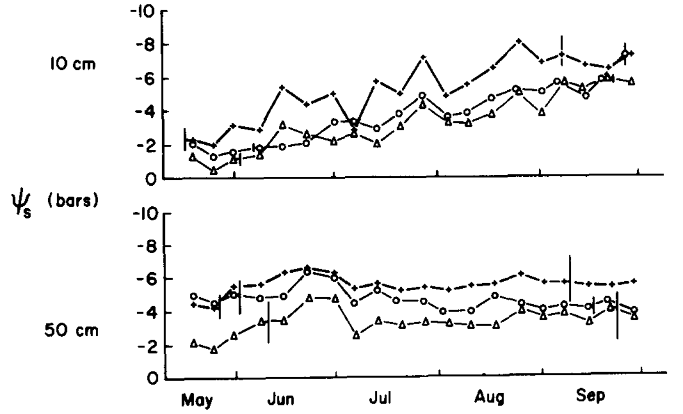

Fig. 1. Seasonal trends in mean soil water potential (ψ_s) in each community within 10 cm and at 50 cm from the marsh surface: (+) mixed; (△) forest margin; (○) creek bank; (|) range of values.

The mixed community always had the most negative mean ψ_s, while the forest margin community had the least negative mean ψ_s.

In contrast to the mean ψ_s at 50 cm depth, the 10 cm depth ψ_s measurements indicate a distinct trend of decreasing ψ_s through the growing season (Fig. 1). At the beginning of the season the ψ_s at 10 cm depth were less negative than at 50 cm, but by the end of the sampling period the situation was reversed. Although an analysis of variance showed that the differences of ψ_s between communities at either the 10 cm depth or 50 cm depth, were statistically significant, it is doubtful whether any ecological significance can be attributed to such small differences.

Plant water potentials

The five plant species could be grouped according to the value and seasonal pattern of ψ_p during the study period. *Iva frutescens*, *Spartina cynosuroides*, and *Panicum virgatum* generally had lower ψ_p values as the season progressed and had mean seasonal dawn ψ_p values of —5.3, —6.0, and —7.5 bar, respectively (Fig. 2). The two sedges, *Scirpus olneyi* and *Scirpus robustus*, rarely had ψ_p values less than —5 bar, showed no distinct seasonal trends in ψ_p, and had seasonal mean ψ_p values of —3.3 and —2.6, respectively (Fig. 2).

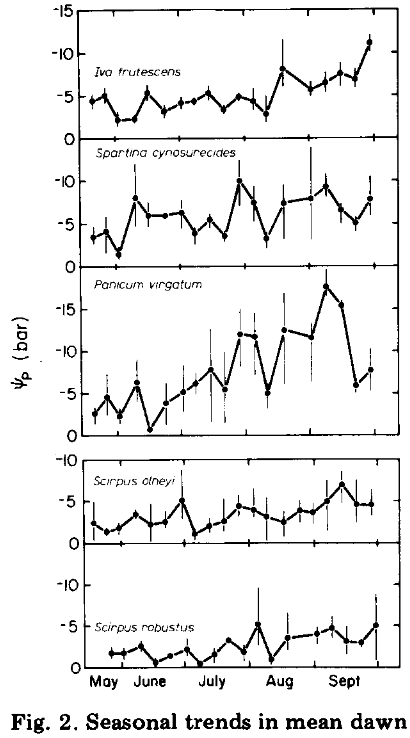

Fig. 2. Seasonal trends in mean dawn plant water potential (ψ_p) values of *Iva frutescens, Spartina cynosuroides, Panicum virgatum, Scirpus robustus* and *Scirpus olneyi*. Vertical bars represent ranges.

DISCUSSION

The differences in ψ_s among the three community types under study were small (Fig. 1). This was true of both the 10 cm depth (within the root zone) and at 50 cm depth (below the root zone). It is difficult to imagine how such small differences in ψ_s could have any effect on species zonation. The small differences in ψ_s between communities may be a result of runoff patterns. Very high rainfall was recorded for May at the beginning of this study (Table I). These rains may have saturated the marsh and provided enough fresh-water runoff to minimize any potential differences in ψ_s of the communities studied. Differences in ψ_s may develop during a very dry year. The rainfall data showed that 1978 was about average for rainfall. In irregularly flooded marshes of North Carolina that are similar to the marsh in the present study, Waits (1967) found great variations in salinity of marsh standing water from one year to the next and that these salinity differences were correlated with differences in rainfall. Thus, the present data do not rule out the possibility that, in dry years, ψ_s differences between communities and between different depths within each community could be greater than were found here. During such years, ψ_s may play a significant part in influencing the species zonation in the Kirkpatrick Marsh.

As measured in this study, ψ_s is probably determined by soil salinity, i.e. increasing salinity produces more negative ψ_s values. North Carolina marshes studied by Waits (1967) had community types that were similar to the communities studied here. His 'mixed' community, dominated by *Spartina patens*, but including *Distichlis spicata* and *Scirpus robustus*, corresponds to the 'mixed' community, and his 'marginal' community type corresponds to the 'marginal' communities of the study reported here. The sequence of community salinity in the North Carolina Marshes was similar to the sequence of ψ_s in Kirkpatrick Marsh, i.e. the mixed community had the highest salinity, and the marginal communities were the least saline. In the North Carolina marsh, the standing water in the mixed community was approximately one-third as saline as the adjacent creek water in a high rainfall year (Waits, 1967).

The differences between ψ_s at 50 cm depth and those measured near 10 cm (see Fig. 1) depth can be attributed to the combined effect of two factors. Concentration of salinity in the root zone as a consequence of evaporative demand by the growing plants could produce a long-term reduction of ψ_s at the 10 cm depth and fresh water flowing beneath the marsh sod from adjacent high ground would dilute any concentration of salts at the 50 cm depth. Harshberger (1911) suggested such a mechanism to account for a salinity gradient between surface and subsurface salt-marsh soil water.

The five species investigated in this study fall roughly into two categories of pre-dawn ψ_p: low ($\psi_p < -5$ bar); and high ($\psi_p > -5$ bar). The three species having $\psi_p < -5$ bar (*Iva frutescens*, *Spartina cynosuroides* and *Panicum virgatum*) were located primarily in the marginal communities and are described elsewhere as being found in fresh to brackish marsh areas and along stream banks (Penfound and Hathaway, 1938; Chapman, 1960; Cooper, 1974; Beal, 1977).

The high water-potential species ($\psi_p > -5$ bar), *Scirpus olneyi* and

Scirpus robustus, are considered to be fresh- to brackish- water marsh species (Penfound and Hathaway, 1938; Cooper, 1974; Beal, 1977). Both species sometimes had ψ_p that were higher than the ψ_s at 10 cm depth but closer to ψ_p at 50 cm depth. Three possible explanations for such results are: (1) infiltration into the leaf tissues of dew formed during the night; (2) sampling errors caused by slicing the leaf or stem tissue (Barrs and Kramer, 1969); and (3), the possibility that these species avoid the effects of low ψ_s by tapping a fresh water supply below 50 cm in the marsh soil. Harshberger (1911) has suggested that the presence of fresh water marsh species in salt marshes was due to their ability to send roots deep enough to find a fresh water source.

As regards the first question implied by the introduction of this paper, "Are there differences between the dawn ψ_p of salt marsh species?", the answer is yes. But, as to the second part of the question, "Do such differences correspond to differences between ψ_s of the communities in which the plants occur?", the answer is unclear. Species having lowest dawn ψ_p occurred in communities having highest ψ_s, and species with highest ψ_p occurred in the community with lowest water potential. This suggests that ψ_s within 50 cm of the surface does not regulate plant species distribution in the tidal marshes of the Rhode River; species with different ψ_p may have root systems at very different depths which are exposed to very different ψ_s. Thus, the recovery level of ψ_p during the night may differ for the different plant species.

ACKNOWLEDGEMENT

This research was supported in part by a grant to the senior author from the Smithsonian Office of Fellowships and Grants.

REFERENCES

Adams, D.A., 1963. Factors affecting vascular plant zonation in North Carolina salt marshes. Ecology, 44: 445—456.
Barbour, M.G. and Davis, C.B., 1970. Salt tolerance of five California marsh plants. Am. Midl. Nat., 84: 262—265.
Barrs, H.D. and Kramer, P.J., 1969. Water potential increase in sliced leaf tissue as a cause of error in vapor phase determinations of water potential. Plant Physiol., 44: 959—964.
Beal, E.O., 1977. A Manual of Marsh and Aquatic Vascular Plants of North Carolina with Habitat Data. North Carolina Agricultural Experiment Station, Raleigh, NC, 298 pp.
Brown, R.W., 1972. Determination of leaf osmotic potential using thermocouple psychrometers. In: R.W. Brown and B.P. Van Haveren (Editors), Psychrometry in Water Relations Research. Utah Agricultural Experimental Station, Logan, UT, pp. 198—210.
Chapman, V.J., 1940. Studies in salt marsh ecology. VI and VII. Comparison with marshes on the east coast of North America. J. Ecol., 28: 118—152.
Chapman, V.J., 1960. Salt Marshes and Salt Deserts of the World. Leonard Hill, London, 392 pp.

Cooper, A.W., 1974. Salt marshes. In: H.T. Odum, B.J. Copeland and E.A. McMahan (Editors), Coastal Ecological Systems of the United States, Vol. 2. The Conservation Foundation, Washington, DC, pp. 55—98.

Hackney, C.T. and De La Cruz, A.A., 1978. Changes in interstitial water salinity of a Mississippi tidal marsh. Estuaries, 1: 185—188.

Harshberger, J.W., 1911. An hydrometric investigation of the influence of sea water on the distribution of salt marsh and estuarine plants. Proc. Am. Philos. Soc., 457: 485.

Mall, R.E., 1969. Soil—water—salt relationships of waterfowl food plants in the Suisun Marsh of California. Calif. Dep. Fish Game, Wildlife Bull., 1: 1—59.

Mendelssohn, I.A. and Marcellus, K.L., 1976. Angiosperm production of three Virginia marshes in various salinity and nutrient regimes Chesapeake Sci., 17: 15—23.

Parrando, R.T., Gosselink, J.G. and Hopkinson, L.S., 1978. Effects of salinity and drainage on the growth of three salt marsh grasses. Bot. Gaz., 19: 102—107.

Penfound, W.T. and Hathaway, E.S., 1938. Plant communities in the marshlands of southeastern Louisiana. Ecol. Monogr., 8: 1—56.

Purer, E.A., 1942. Plant ecology of the coastal salt marshlands of San Diego County, California. Ecol. Monogr., 12: 81—111.

U.S. Department of Commerce, 1978. Climatological Data Annual Summary, Natural Climatic Center, MD, Vol. 82, No. 13.

Waits, E.D., 1967. Net primary productivity-of an irregularly-flooded North Carolina salt marsh. Ph.D. Thesis, North Carolina State University, Raleigh, NC, 113 pp.